

INVASION OF *CARPOBROTUS EDULIS* AND  
*SALIX LASIOLEPIS* AFTER FIRE IN A  
COASTAL CHAPARRAL SITE IN  
SANTA BARBARA COUNTY,  
CALIFORNIA

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ABSTRACT

Observations in permanent plots after a 1982 controlled fire in chaparral vegetation in coastal Santa Barbara County, California demonstrate that *Carpobrotus edulis*, the common introduced ice plant, increased substantially along with other native plants capable of invading disturbed sites such as *Salix lasiolepis*. Although fire is a natural disturbance, it can favor the spread of invasive exotics when a seed source is available. Controlled burning programs must consider the possibility and risks of invasion by exotics.

The importance of human disturbances such as grazing, agriculture, and road construction in promoting the invasion of exotics is well known (Elton 1958). It is less clear if natural disturbance factors such as fire hinder or assist invasion (Johnstone 1986). A well-accepted explanation for weed invasion is that human disturbance creates a new environment in which the native plants are at a disadvantage with respect to invaders. Thus, the argument can be made that fire in a landscape where it has a long history should not give an advantage to exotics. On the contrary, the native plants, which are presumably fitted to the special local characteristics of the fires, might be favored. This theoretical reasoning is given practical support by burning experiments that have shown a decrease in exotics (e.g., Hillyard 1985). It is the purpose of this paper to demonstrate that burning by no means inevitably favors natives and may, in some instances, promote the spread of exotics.

The exotic studied here, *Carpobrotus edulis* (L.) Bolus ("ice plant"), has been widely planted in California and is now viewed as a weed (McClintock 1985) that should be eradicated in sensitive natural habitats (e.g., Libby 1979). It is particularly aggressive in sandy coastal sites (Griffin 1978), where it can become the dominant plant over large areas. Populations of an exotic succulent plant such as *C. edulis* might be expected to decrease with burning, and fire might be expected to serve as a means of controlling this species. Our results show, on the contrary, that fire can favor its expansion.

### STUDY AREA

The study was conducted on Burton Mesa in Santa Barbara County, California (34°42'30"N, 120°43'W) about 2.6 km from the ocean to the west of the railroad tracks near the intersection of 35th Street and California Boulevard on Vandenberg Air Force Base. The soil type at the site is mapped as Tangair with inclusions of the poorly-drained Narlon series (Shipman 1972). Both soils have coarse sandy loam textures, are derived from marine deposits, and are low in fertility.

The vegetation at the site is a distinctive central-coast phase of chaparral. It is characterized by low, sometimes salt-spray trimmed canopies of evergreen species with an admixture of drought-deciduous coastal sage scrub elements. The site also includes other species of limited or disjunct distribution, such as *Arctostaphylos rudis* and *Eriodictyon capitatum*.

### METHODS

The data reported here were collected in conjunction with an experimental burn of approximately 40 ha conducted in the summer of 1982 to determine the effect of prescribed fire on *E. capitatum* (Jacks, Zedler, and Scheidlinger unpubl. report). Before the fire, a sample area of approximately 0.6 ha, delimited by clearing along a paved road, a railroad track, and an old unpaved track, was selected and divided into two plots of about 2500 and 3600 sq m, the larger of which was left unburned. A 100 m transect, crossing both the burned and unburned vegetation, was established in June 1982 before the fire and was sampled for crown cover. In addition to marking individual *E. capitatum* to follow in survivorship studies, we established four 3 × 3 m plots in the burn area centered on *E. capitatum* clumps. These plots were therefore not random with respect to *E. capitatum* but were not selected with reference to *C. edulis*. The cover of all shrub species within these plots was recorded and the locations of all *E. capitatum* were mapped before the fire. After the fire, seedlings and sprouts were mapped.

We estimated seed production of *C. edulis* in 1985 by counting the number of fruits in 40 regularly spaced meter-square quadrats, collecting 3 fruits from each quadrat in which they were present, and counting the seeds in a randomly selected sub-sample of 12 fruits.

### RESULTS

In 1982, before the fire, *C. edulis* was present along the road and the railway that bordered the site. No *C. edulis* plants were recorded within the experimental area, however, which had a nearly complete

TABLE 1. PRE- AND POST-BURN COVER OF SHRUBS, SUB-SHRUBS, AND *Carpobrotus edulis* ON A CHAPARRAL SITE ON VANDENBERG AIR FORCE BASE, SANTA BARBARA COUNTY, CALIFORNIA. Transect lengths were 60 m for 1982 and 100 m for 1985. Live cover values include overlap. Bare ground is area not covered by live or dead plant canopies. Nomenclature after Smith (1976).

Species	Pre-burn 1982 cover (%)		Post-burn 1985 cover (%)	
	Live	Dead	Live	Dead
<i>Adenostoma fasciculatum</i>	45.3	1.2	4.3	0.0
<i>Arctostaphylos purissima</i>	39.3	0.3	1.1	0.0
<i>Arctostaphylos rudis</i>	15.9	1.7	1.0	0.0
<i>Carex</i> sp.	0.0	0.0	0.3	0.0
<i>Carpobrotus edulis</i>	0.0	0.0	26.2	0.3
<i>Ceanothus impressus</i>	0.0	0.0	0.1	0.0
<i>Ceanothus ramulosus</i>	1.2	2.6	0.5	0.0
<i>Eriodictyon capitatum</i>	3.2	1.2	1.7	0.0
<i>Haplopappus ericoides</i>	1.0	0.1	0.0	0.0
<i>Helianthemum scoparium</i>	0.0	0.0	30.4	1.9
<i>Lotus scoparius</i>	0.0	0.0	3.0	0.9
<i>Salvia mellifera</i>	3.9	0.4	3.6	0.0
Bare ground	1.8	—	33.1	—

cover of living or dead shrub canopies of primarily evergreen species (Table 1). Because of this dense cover, we cannot assert that *C. edulis* was not present somewhere in the experimental area, but there is no doubt that its total density was negligible. In contrast, in 1985, three years after the fire, the cover of *C. edulis* was 26%, making it the second-most prevalent post-fire perennial plant (Table 1).

Observations in the permanent plots confirm that seedling establishment is responsible for the increase in *C. edulis*. These plots were resampled in 1983, and the location of *C. edulis* and shrub seedlings was recorded (Table 2). Seedlings of *C. edulis* were recorded at an average density of over 7000/ha. A 1985 resample relocated 70% of these, indicating a high survivorship. Three new plants of *C. edulis* were found in 1985 that may have been established in the second season of recovery but more probably were missed in the initial survey.

Although *C. edulis* has been reported to reproduce only vegetatively (McClintock 1985), the observed seedling establishment obviously contradicts this. We collected fruits and found an average of 5.3 (s.d. = 12.1, n = 40) fruits/m<sup>2</sup> and an average of 1004 seeds/fruit (s.d. = 431, n = 12). This indicates a 1985 seed production of over 5.3 million seeds/ha. This figure can be expected to vary from year to year and place to place, but the numbers serve to show that *C. edulis* can have prodigious seed production.

Coastal sage scrub communities are particularly vulnerable to changes in species composition (i.e., invasion) when, as in this case,

TABLE 2. ABUNDANCE OF SEEDLINGS IN PERMANENT QUADRATS NOTED IN JULY 1983 AFTER THE SUMMER 1982 PRESCRIBED BURN. Values are based on averages of four 3 × 3 m plots. s.e. represents the standard error of the mean for the sample of four plots.

Species	Number/ha	s.e.
<i>Arctostaphylos rudis</i>	2230	4450
<i>A. purissima</i>	41,075	18,000
<i>Adenostoma fasciculatum</i>	1650	1650
<i>Salvia mellifera</i>	6930	2700
<i>Ceanothus ramulosus</i>	825	830
<i>C. impressus</i>	1375	1380
<i>Salix lasiolepis</i>	6400	715
<i>Baccharis pilularis</i>	4425	1211
<i>Lotus scoparius</i>	3600	1895
<i>Carpobrotus edulis</i>	7780	2100
<i>Solanum xantii</i>	4700	1470

the vegetation is composed mainly of species with no ability (e.g., *Ceanothus ramulosus*, *Arctostaphylos purissima*) or only a weak ability (e.g., *Salvia mellifera*) to resprout after fire (Westman and O'Leary 1986). The establishment of several other species is evidence of this susceptibility of burned coastal sage chaparral to invasion. The presence of seedlings of *Salix lasiolepis* in the burned area was very unexpected (Table 2). No mature individuals of this species were observed anywhere within a kilometer of the site before or after the fire. The identity of the species was confirmed, however, by comparison with seedlings found along the Santa Ynez River, where the species is very abundant. We assume that the seeds were blown onto the site from these large stands along the Santa Ynez River which lies about 2 km to the south.

It is not surprising that willow seeds dispersed to the site and germinated there. What is more remarkable is that they established and survived to early July 1983, and that a few were still present and alive in the area the following summer. The mortality in the permanent plots was, however, complete by the second summer. The initial survival of the willows probably was aided by the fact that the 1982–83 hydrologic year for the area was one of above-normal precipitation (81.9 cm; mean rainfall is 35.2 cm), and it may have been enhanced by the presence of a heavy clay layer overlying shale bedrock that underlies the sandy surface soil at a depth of a meter or more. The clay layer may have allowed high moisture conditions to persist in the first summer. This wet year was followed by 2 years of below-average precipitation (1983–84, 21.6 cm; 1984–85, 26.5 cm) which, in part, may explain the lack of willow establishment.

Other exotic species besides *C. edulis* were observed in the burn area. A number of *Eucalyptus* sp. seedlings, whose seeds evidently



dispersed from a nearby windbreak, were present as were the exotics *Cortaderia* sp. and *Herrea elongata*.

Two readily dispersed native species, *Baccharis pilularis* (wind-dispersed) and *Solanum xantii* (animal-dispersed) were common as seedlings in the post-fire vegetation (Table 2) even though they were minor elements as mature shrubs before the fire. These species are frequent in chaparral and coastal sage scrub, and it is questionable whether their presence constitutes "invasion".

#### DISCUSSION

The substantial cover of *C. edulis* after the 1982 fire is evidence that the invasion of exotic species into native vegetation can be advanced, rather than retarded by burning. The success of *C. edulis* as an invader is probably explained by its evolution with fire. Observations on *Carpobrotus* spp. in South Africa and Australia, where they are native, show that they often establish from seed after fire. Eugene Moll (pers. comm. 1985) of the University of Cape Town has noted post-fire seedling establishment of *C. dinidiata* in the sand plain and mesic mountain fynbos communities in South Africa, although he notes that the species is most abundant in communities that are seldom burned. Judith Brown of the Western Australian Wildlife Research Centre (pers. comm. 1985) reports that *C. edulis*, also introduced into W. Australia, establishes by seed after hot fires in coastal locations near Perth, although in her opinion it is "not an aggressive colonizer". Native species of *Carpobrotus*, however, can invade woodlands after fire. In one case on Middle Island off the coast of W. Australia a thick carpet of *Carpobrotus* developed from seedlings after fire in a *Eucalyptus angulosa*-*E. platypus* forest unburned for 170 years. This evidence suggests that invasion of *C. edulis* into burned chaparral at Vandenberg AFB may not be as anomalous as it appears.

Although fire provided the "temporary invasion window" (Johnstone 1986) there must also be propagules to exploit it. We do not know how and when the seeds of *C. edulis* dispersed to the site. Fruits of *C. edulis* are eaten by small mammals (W. Ferren pers. comm.) and the seeds are small and hard-coated. We suspect that most of the seeds were deposited at the site in small mammal feces. Therefore, the majority of the seeds probably were in the soil for some time before the fire.

It is known that fire can be used to decrease exotics in coastal settings. W. James Berry of the State Department of Parks and Recreation (pers. comm. 1985) reports several successes in controlling introduced species—*Avena* at Pt. Mugu and Malibu, *Bromus diandrus* at Montaña de Oro, and *Brassica* at Pt. Lobos. Timing was a key element in these efforts. The burns were conducted when they

would kill most of the seed crop of the exotics without seriously harming the desirable species, mostly perennial natives.

Our observations make it clear that these successes must not be taken as an indication that fire will inevitably act to the favor of natives over exotics. A case in point comes from South Africa where the native vegetation is well adapted to survive fire, but invasion of exotics, including pines from the Northern Hemisphere and *Hakea* from Australia, has become a serious problem. Fire can be used to reduce the abundance of some of these invaders, but others (e.g., *Acacia*) cannot be eliminated with burning (Kruger and Bigalke 1984).

It is also apparent that edge effects were important in the situation we describe. Human disturbance along the margins of the experimental plot allowed the populations of *C. edulis* to establish and maintain themselves. Fire provided the opportunity for the seedlings to establish. These results underline the importance of minimizing edge to area ratios in retarding the expansion of exotics. They also suggest that longer fire rotations should be favored over shorter rotations when undesirable exotics that require open conditions for establishment are present.

#### ACKNOWLEDGMENTS

We thank Clay Gautier and Paul Jacks for help in sampling and data analysis, and Jim Johnston and others at Vandenberg AFB for funding and assistance. F. Davis, M. Carroll, W. Ferren, and D. Keil made helpful comments on the manuscript. This project was funded by AFOSR grant #84-0284, the U.S. Fish and Wildlife Service Office of Endangered Species, and NSF Grant BSR-8507699.

#### LITERATURE CITED

- ELTON, C. S. 1958. The ecology of invasions by animals and plants. Chapman and Hall, London.
- GRIFFIN, J. R. 1978. Maritime chaparral and endemic shrubs of the Monterey Bay region, California. *Madroño* 25:65-112.
- HILLYARD, D. S. 1985. Weed management in California's State Park system. *Fremontia* 13:18-19.
- JOHNSTONE, I. M. 1986. Plant invasion windows: a time-based classification of invasion potential. *Biol. Rev.* 61:369-394.
- KRUGER, F. J. and R. C. BIGALKE. 1984. Fire in fynbos. In P. de V. Booysen and N. M. Tainton, eds., *Ecological effects of fire in South African ecosystems*, Chapter 5, p. 67-114. Springer-Verlag, Berlin.
- LIBBY, J. 1979. Chapter weed reports: *Acacia* and pampas grass in Santa Cruz. *Fremontia* 6:19-20.
- MCCLINTOCK, E. 1985. Escaped exotic weeds in California. *Fremontia* 12:3-6.
- SHIPMAN, G. E. 1972. Soil survey of the northern Santa Barbara area. U.S.D.A. Soil Conservation Service, Washington, DC.
- SMITH, C. F. 1976. A flora of the Santa Barbara region, California. Santa Barbara Museum of Natural History, Santa Barbara, CA.
- WESTMAN, W. E. and J. F. O'LEARY. 1986. Measures of resilience: the response of coastal sage scrub to fire. *Vegetatio* 65:179-189.

(Received 29 May 1987; revision accepted 10 Feb 1988.)